Competition–defense tradeoffs and the maintenance of plant diversity

David V. Viola[1], Erin A. Mordecai, Alejandra G. Jaramillo, Seeta A. Sistla, Lindsey K. Albertson, J. Stephen Gosnell, Bradley J. Cardinale, and Jonathan M. Levine

Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, CA 93106

Ecologists have long observed that consumers can maintain species diversity in communities of their prey. Many theories of how consumers mediate diversity invoke a tradeoff between species' competitive ability and their ability to withstand predation. Under this constraint, the best competitors are also most susceptible to consumers, preventing them from excluding other species. However, empirical evidence for competition–defense tradeoffs is limited and, as such, the mechanisms by which consumers regulate diversity remain uncertain. We performed a meta-analysis of 36 studies to evaluate the prevalence of the competition–defense tradeoff and its role in maintaining diversity in plant communities. We quantified species' responses to experimental resource addition and consumer removal as estimates of competitive ability and resistance to consumers, respectively. With this analysis, we found mixed empirical evidence for a competition–defense tradeoff; in fact, competitive ability tended to be weakly positively correlated with defense overall. However, when present, negative relationships between competitive ability and defense influenced species diversity in the manner predicted by theory. In the minority of communities for which a tradeoff was detected, species evenness was higher, and resource addition and consumer removal reduced diversity. Our analysis reframes the commonly held notion that consumers structure plant communities through a competition–defense tradeoff. Such a tradeoff can maintain diversity when present, but negative correlations between competitive ability and defense were less common than is often assumed. In this respect, this study supports an emerging theoretical paradigm in which predation interacts with competition to both enhance and reduce species diversity.

meta-analysis | resource limitation | predation | species diversity

Identifying processes that maintain species diversity in the face of competitive exclusion is a key goal of ecology (1). Because consumers can alter the outcome of competition between their prey, consumer-based mechanisms are commonly invoked to explain species coexistence (2–4). Many empirical (5–7) and theoretical studies (8–10) have suggested that consumers maintain species diversity when predation differentially harms superior competitors. For example, Lubchenco (3) showed that snail herbivory increased algal diversity in tide pools only when preferred prey were also the competitive dominant. Similar requirements for consumers to maintain diversity of their prey have been formalized in mathematical models: when competing species share both resources and consumers, coexistence is possible only if the prey species that are superior competitors for resources are also less resistant to predation (9, 10).

However, a large gap has developed between the empirical evidence supporting this theoretical tradeoff and its application to explain how consumers regulate real communities. For the many studies that have invoked a tradeoff between competitive ability and defense against consumers, the mechanism is more often assumed than directly demonstrated (11). Few studies have evaluated the strength of this tradeoff across species (12–14), largely due to the challenge of quantifying species' abilities to compete for resources and to defend themselves against consumers. Instead, many studies that have been put forth as support for the tradeoff

actually focus on trait differences between individuals of a single species (ref. 11 and references therein). Such studies offer only limited insight into the operation of the tradeoff at the community level (i.e., across species). Therefore, though it is clear that consumers have some effect on species diversity, it remains unclear whether a competition–defense tradeoff is a widespread mechanism underlying consumer effects.

In this paper, we describe a 36-study meta-analysis conducted to quantify the relationship between competitive ability and defense and to evaluate its role in maintaining species diversity in plant communities. Plants use several types of defenses to protect themselves against consumers. However, we focus solely on the resistance component of defense, because past theoretical work has made clear that only a tradeoff between competitive ability and resistance promotes coexistence (9, 15) (*SI Text*). We adopt an approach that allows us to estimate competitive ability and defense across numerous studies. Specifically, we infer competitive ability and resistance to consumers by quantifying species' responses to experimental resource addition and consumer removal, respectively (Figs. 1 and 2). Because numerous studies have simultaneously manipulated these factors, this approach dramatically expands the pool of studies available for examining tradeoffs. Furthermore, because it was not the original intent of such studies to assess the competition–defense tradeoff, these studies provide what can be considered unbiased estimates of the relationship between competitive ability and resistance to consumers.

Our approach relies on the expectation that the species most sensitive to the limiting resources, the poorest competitors, benefit most from resource addition (16). Likewise, those most limited by predation benefit most from consumer removal. Therefore, if a competition–defense tradeoff exists, the species that respond most strongly to resource addition will respond least strongly to consumer removal, and vice versa (Fig. 1). These expectations reflect a common theoretical view of how populations respond when the intensity of resource limitation or consumer pressure changes (8–10, 16). Models incorporating competition–defense tradeoffs have shown that when resource availability and consumer pressure are low, communities are dominated by the species that are superior at obtaining resources but vulnerable to consumers (9, 10). As resource availability and consumers increase, dominance shifts to resistant species that are poor at resource exploitation. If the resource and consumer manipulations used in our meta-analysis studies are viewed as discrete points along the continuous gradients used in such models, then increasing resource availability would benefit poor competitors, and reducing consumer pressure would benefit species vulnerable to predation. Indeed, there is
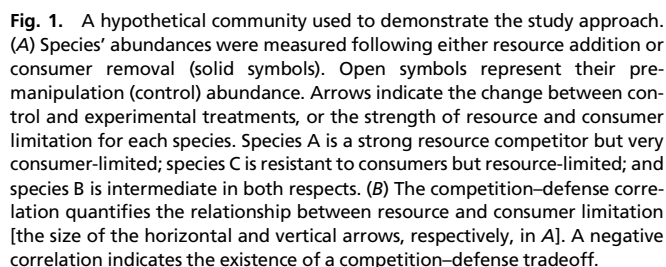
ECOLOGY

Fig. 1. A hypothetical community used to demonstrate the study approach. (*A*) Species' abundances were measured following either resource addition or consumer removal (solid symbols). Open symbols represent their pre-manipulation (control) abundance. Arrows indicate the change between control and experimental treatments, or the strength of resource and consumer limitation for each species. Species A is a strong resource competitor but very consumer-limited; species C is resistant to consumers but resource-limited; and species B is intermediate in both respects. (*B*) The competition–defense correlation quantifies the relationship between resource and consumer limitation [the size of the horizontal and vertical arrows, respectively, in *A*]. A negative correlation indicates the existence of a competition–defense tradeoff.

strong empirical support that species' responses to the experimental manipulations conform to our expectations about resource and consumer limitation (17–19). For example, competitive ability of 27 grassland species was negatively correlated with their increase in abundance along a fertilization gradient (18).

We have tested our expectations using simulations of one of the foremost models underlying the competition–defense tradeoff (see *SI Text* for full details). The model (9) is based on the common R^* framework of competitive ability, where R^* is the level to which a species depletes resources when grown in monoculture (16). Species strongly limited by resources have high R^*s. Likewise, P^* is the consumer density that a prey species can support in monoculture, with large values reflecting strong consumer limitation (9). We imposed perturbations in resource supply and consumer mortality on two competing species with a tradeoff between resource and consumer limitation (Figs. S1 and S2). The change in both species' densities relative to their preperturbation densities supports our expectations (Fig. 2). The species that is more limited by consumers (species 1) benefited more from increasing consumer mortality (Fig. 2*A*), whereas the species more limited by resource availability (species 2) benefited more from resource addition (Fig. 2*B*). In *SI Text*, we also show that this result is robust to our specific parameter selection (Fig. S3).

To assess whether similar trends are evident in empirical studies, we quantify the strength of the competition–defense tradeoff as the correlation between species' responses to resource addition and consumer removal (the competition–defense correlation; Fig. 1*B*). Negative correlations indicate the existence of a tradeoff. Because the influence of resources and consumers on prey diversity may depend on factors that varied across studies (20), we examine competition–defense correlations of studies partitioned by the characteristics of the species and systems in-
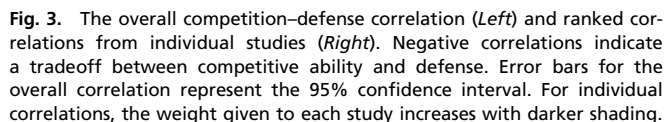

Fig. 2. Responses of two species with a competition–defense tradeoff to simulated perturbations in resource supply and consumer mortality. The responses in the large panels are species' log response ratios relative to their preperturbation densities (defined at $t = 250$). Perturbations are included for reference in the small panels. (*A*) The species more limited by predation (species 1) benefits more from the decrease in consumer pressure than the resistant species (species 2). (*B*) The poor resource competitor (species 2) benefits more from resource addition than the strong resource competitor (species 1). See *SI Text* for a full description of the model.

volved (Table S1). Finally, we test the theoretical prediction that the tradeoff maintains diversity (9, 10). Specifically, we use our dataset to test the following hypotheses: (*i*) diversity of plant communities increases with the strength of the competition–defense tradeoff; and (*ii*) in communities for which a tradeoff is observed, removal of competition or predation reduces plant species diversity. As we will show, evidence for a widespread competition–defense tradeoff is equivocal. Even so, the relationship between competitive ability and defense against herbivores still yields valuable insight into the processes that regulate diversity within plant communities.
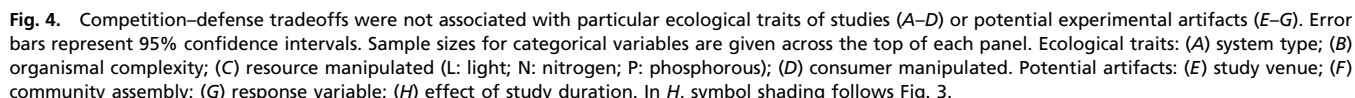
Results

In contrast to theoretical predictions, the correlation between plant species' response to resource addition and their response to consumer removal was positive when averaged across all studies. Though the overall correlation was significantly positive ($P = 0.046$), it was relatively small in magnitude and resulted from the fact that only slightly more studies showed positive correlations than had the theoretically expected negative correlation (Fig. 3; of the 36 studies, 13 exhibited a negative correlation between species' responses to resource addition and to consumer removal, as is predicted by a tradeoff). Combined correlations were qualitatively unaffected by whether studies were weighted or not weighted to account for certainty in measurements, and they were not affected by the choice of the time point that was analyzed for studies with

Fig. 3. The overall competition–defense correlation (*Left*) and ranked correlations from individual studies (*Right*). Negative correlations indicate a tradeoff between competitive ability and defense. Error bars for the overall correlation represent the 95% confidence interval. For individual correlations, the weight given to each study increases with darker shading.

time-series data available (*Methods*). Taken as a whole, these findings suggest that a competition–defense tradeoff is far from a ubiquitous feature of plant communities. Rather, our analysis suggests that plant species that are the better competitors tend, on average, to be more resistant to the impacts of consumers.
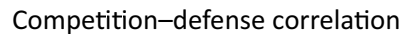
We attempted to determine if measured correlations varied in strength either with the specific type of organism and habitat being considered or with the design of the experiment and how response variables were measured (see Table S1 for a full list of factors considered). However, we were unable to find any associations between ecological or experimental variables and the strength of the competition–defense tradeoff. In fact, most combined correlations remained positive when the dataset was partitioned by category, and there were no significant differences between levels of any categorical effect (Fig. 4 and Tables S2 and S3). There was, however, an association between the abundance hierarchy of plants and the strength of the tradeoff. We partitioned each community into subsets of common and rare species, represented by the four most common and four least common species in each study, respectively. Mean correlations averaged across all studies did not differ between common and rare subsets

($P = 0.442$; Fig. S4*A*). In contrast, rare species correlations were consistently lower than those for common species when they were compared within each study ($P = 0.045$; Fig. S4*B*), implying that the competition–defense tradeoff is stronger among the rarest species in a community.

Despite the heterogeneity in correlations over all studies, the relationship between competitive ability and defense did influence species diversity in ways predicted by theory. We measured the change in diversity due to both resource and consumer manipulations, and then determined the relationship between these responses and the competition–defense correlation. Both resource addition and consumer removal decreased species evenness in communities with a competition–defense tradeoff, and increased evenness in communities without a tradeoff (Fig. 5 *A* and *B*). Both manipulations also tended to decrease species richness when a competition–defense tradeoff was present, but increase richness when the tradeoff was not present, although these effects were nonsignificant (Fig. 5 *C* and *D*). We also found that in the unmanipulated communities, species evenness was greater in systems with a competition–defense tradeoff than in those without (Fig. 6*A*). There was no significant association between the competition–defense tradeoff and richness (Fig. 6*B*).

Discussion

We found varied empirical support for a tradeoff between plant species' ability to compete for resources and their defense against consumers. A slight majority of studies in our analyses showed a pattern opposed to the expected tradeoff: strong competitors tended to be more resistant to consumers. However, competition–defense correlations were highly variable overall and were evident in a minority of systems. Regardless of whether competition–defense correlations were negative or positive, the relationship between competitive ability and defense affected diversity in ways that are consistent with ecological theory. Diversity tended to be higher in studies with negative competition–defense correlations than in those with positive correlations, suggesting that the competition–defense tradeoff does function as a diversity maintenance mechanism where it occurs. For communities with a tradeoff, adding resources or removing consumers reduced diversity because the factors preventing individual species from becoming superabundant had been removed. For communities with positive competition–defense correlations, resource addition

Fig. 4. Competition–defense tradeoffs were not associated with particular ecological traits of studies (*A–D*) or potential experimental artifacts (*E–G*). Error bars represent 95% confidence intervals. Sample sizes for categorical variables are given across the top of each panel. Ecological traits: (*A*) system type; (*B*) organismal complexity; (*C*) resource manipulated (L: light; N: nitrogen; P: phosphorous); (*D*) consumer manipulated. Potential artifacts: (*E*) study venue; (*F*) community assembly; (*G*) response variable; (*H*) effect of study duration. In *H*, symbol shading follows Fig. 3.

Fig. 5. Experimental manipulations decrease evenness in communities with competition–defense tradeoffs and increase evenness in communities without tradeoffs. (*A* and *B*) Evenness and (*C* and *D*) richness responses to resource addition and consumer removal as functions of the competition–defense correlation. Diversity responses are the log response ratios of diversity in manipulated relative to unmanipulated communities. R^2 and P values are from weighted linear regressions. Best fit lines for models significant at the α = 0.05 level are shown. Symbol shading follows Fig. 3.

and consumer removal tended to increase diversity through differential benefits to species that were both poor resource competitors and poor at withstanding predators. Thus, though competition–defense tradeoffs were not as common as has been assumed previously, when that tradeoff is present, the main predictions of how resources and consumers interactively influence species diversity were supported by this dataset.

Potential Limitations. Like all meta-analyses, several limitations of our dataset should be kept in mind when interpreting the results. First, our analyses assume that investigators correctly identified the resources and consumers that most limited populations in a given system. Though we cannot verify conclusively that this assumption is valid, additional analyses offer strong support for it. Both resource addition and consumer removal increased community biomass relative to unmanipulated conditions (mean log response ratio for resource addition = 0.47, 95% CI: 0.15–0.79; mean log response ratio for consumer removal = 0.31, 95% CI: 0.14–0.49), which suggests that the resources and consumers manipulated were in fact limiting species' population growth.

Our conclusions may also be constrained by the species composition that investigators selected for their focal communities. For example, a tradeoff within a particular subset of species may have been masked by the inclusion of additional species differentiated along other niche axes (i.e., those not associated with shared resources or consumers, such as might occur for species that coexist through a competition–colonization tradeoff). Alternatively, species that are poor at both resource acquisition and defense, and thus that are being slowly excluded, may likewise obscure the detection of a tradeoff within the subset of species that stably coexist. Our observation that competition–defense correlations are more negative for the rarest species in a community provides evidence that the strength of a tradeoff can differ between subsets of ecologically similar species. This finding may reflect the fact that species less subject to a competition–defense tradeoff, and therefore capable of being both resistant to con-

sumers and good resource competitors, become more common than those species constrained by the tradeoff.

Alternatives to the Competition–Defense Tradeoff. Many mechanisms have been proposed to explain the maintenance of species diversity, so it should not be a surprise that the competition–defense tradeoff is absent from some plant communities. Indeed, tradeoffs in requirements for multiple resources; tradeoffs between competitive ability and colonization ability; and temporal or spatial variation in the environment are just a few additional mechanisms that can stabilize plant species assemblages (reviewed

Fig. 6. Species diversity tends to higher in communities with a competition–defense tradeoff. (*A*) Evenness and (*B*) richness in unmanipulated communities. R^2 and P values are from weighted linear regressions. Best fit lines for models significant at the α = 0.05 level are shown. Symbol shading follows Fig. 3.

Viola et al.

in refs. 1 and 11). In many cases, these coexistence mechanisms may operate in concert with the competition–defense tradeoff, or, for communities lacking a competition–defense tradeoff, they may serve as the primary determinants of plant diversity. Because the competition–defense tradeoff was originally conceived to explain how consumers could maintain the diversity of their prey, we focus our attention on consumer-based mechanisms and ask two important questions. First, why is the competition–defense tradeoff not more prevalent? And second, what mechanisms other than the competition–defense tradeoff could explain the beneficial effects of consumers on species diversity?

We propose a simple explanation for why a competition–defense tradeoff is not more common. The mechanistic basis of this tradeoff stems from a larger body of work on allocation-based tradeoffs at the level of the individual. Given that all individuals have finite resources at their disposal, they must strike a balance between investment in resource acquisition and investment in defense. However, for individual-level allocation tradeoffs to extend to whole communities and thereby maintain diversity, individuals of all species must have a similar resource stock (i.e., allocation constraint) to allocate toward competitive ability or toward defense. Our findings may reflect the fact that all species in a community do not share the same constraints. Alternatively, some traits, such as low nitrogen content in a nitrogen-limited system, may simultaneously confer both increased competitive ability and consumer resistance (21).

How can we reconcile our results with empirical work showing that consumers increase species diversity at lower trophic levels (2, 3, 20)? An emerging paradigm emphasizes that the overlap between species in their resource use and in their consumer assemblages is key to understanding when and how consumers will benefit diversity (22). In communities with a competition–defense tradeoff, shared consumers promote diversity by balancing resource and consumer limitation across species. However, in many cases consumers may regulate diversity through other mechanisms in which competition and predation combine to either promote or undermine species coexistence (22). For example, when consumers are specialists rather than generalists, predation can still maintain diversity in the absence of a tradeoff via a Janzen–Connell mechanism (23, 24). Here, each species supports consumer populations that differentially harm themselves relative to their competitors. Whether the competition–defense tradeoff and other consumer-based coexistence mechanisms extend beyond plants to higher trophic levels is uncertain because complex behavioral traits may underlie competitive ability and resistance. However, Holt et al. (9) have speculated that, for animal prey, increased mobility might simultaneously increase the prey species' resource uptake rate as well as its predation risk. In such a case, the competition–defense tradeoff could apply equally well to animal species.

Our finding that the competition–defense tradeoff is not widespread in plant communities also has more general implications for future research. Although the tradeoff certainly maintains diversity in some systems, ecologists should not simply presume that predation maintains diversity via this tradeoff without explicitly evaluating species' competitive ability and defense against consumers. However, regardless of whether a tradeoff is present, the relationship between competition and defense does influence species diversity in expected ways, supporting the theoretical predictions. Continued work quantifying the relationships between competitive ability and defense will add to our knowledge of the mechanisms by which abiotic and biotic factors interact to regulate diversity.

Methods

Data Collection. Our dataset was compiled from studies identified by searching the ISI Web of Science using the search terms [resourc* or nutrient* or fertili*] and [herbivor* or graz* or consum*]. These were the same strings used in recent meta-analyses of community regulation by consumer and nutrient limitation (20, 25). We also included the publications used in these analyses in our pool of potential studies. Studies were only included in our dataset if they met the following criteria: (*i*) The experimental community was composed of at least three plant species, the minimum required to obtain meaningful correlations between species' responses to resource addition and consumer removal. (*ii*) Resource availability (light, nitrogen, phosphorous, or combinations thereof) was directly manipulated and (*iii*) consumer abundance was directly manipulated. Studies that compared communities in different habitats that varied naturally in resource availability or consumer pressure were not included because of potential confounding effects. And (*iv*) authors reported species-specific responses (rather than aggregate community responses) to resource and consumer treatments and corresponding measures in control plots. In some instances, authors reported observations from multiple sites, time periods, or under different experimental conditions. These observations were considered independent studies for our purposes. Ultimately, we incorporated 36 studies from 26 separate publications into our dataset. Citations for these publications are provided in *SI Text*.

When studies reported multiple observations over time (seven studies), we recorded responses at all time points (Fig. S5) but performed our analyses on the first time point only. For these seven studies, we fit a mixed model to determine if competition–defense correlations changed over time (days since start of treatments, log transformed), with study included as a random effect. There was no effect of time (likelihood-ratio test: $\chi^2 = 0.03$, df = 1, $P = 0.87$). To confirm that the choice of time point did not influence our results, we also conducted our analyses using the final time point and reached the same conclusions.

Data were extracted either from tables or from digitized figures using DigitizeIt 1.5.8. Our primary data were species abundances in both experimental and control treatments (solid and dashed symbols in Fig. 1*A*, respectively). We then inferred competitive ability and sensitivity to predation as the response of a species to resource addition and consumer removal, respectively (i.e., analogous to the arrows in Fig. 1*A*; see following section and *SI Text*). Species richness and evenness (the E_{var} index) (26) were also calculated. In addition to these quantitative data, categorical information about each study was collected to determine if observed competition–defense tradeoffs varied depending on ecological or experimental factors. A complete list of all variables and their definitions is given in Table S1.

Meta-Analysis. We quantified species' responses to resource addition and their responses to consumer removal as the proportional change in abundance between experimental and control treatments using log response ratios (27). To detect a tradeoff using this approach, we estimated the response to resource addition when consumers were unmanipulated and the response to consumer removal when resources were unmanipulated (i.e., the responses are orthogonal; Fig. 1*A*). A common problem with the log response ratio is that zero values of the response variable cause the log ratio to be undefined, and in our dataset, species were occasionally absent in some treatments. We considered zero values as potentially meaningful responses that should not be eliminated, and we corrected them by adding the lowest value of the response variable observed within a study to all observations for that study. This correction yields a conservative estimate of the log response ratio for species that decline below detection limits or have gone extinct.

To quantify the magnitude of a tradeoff in a given study, we calculated the correlation (i.e., the competition–defense correlation) between species' responses to resource addition (the inverse of competitive ability) and to consumer removal (the inverse of resistance to consumers) as our effect size metric, with negative correlations indicating a tradeoff (Fig. 1*B*). We tested whether the competition–defense correlation differed from zero with mixed-effects models (27). Correlation coefficients were *z*-transformed to improve normality (28) and combined across studies with study included as a random effect (29). We weighted studies by the inverse of the sampling variance of their effect sizes, as recommended by Hedges et al. (27), to account for the greater certainty in studies with less variation. In addition to the main model that estimated the mean correlation across all studies, we fit separate models that included fixed categorical effects (Table S1) to account for variability attributable to the ecological or experimental characteristics of each study. Models were fit using the metafor package (29) in R 2.10.1 (www.R-project.org).

To determine how the strength of the competition–defense tradeoff varied with species' abundance in the community, we examined the subset of studies that were most speciose (eight or more species, *n* = 17) and ranked species by their abundance under control conditions. We designated the four most abundant species as common and the four least abundant as rare, and then calculated competition–defense correlations within each study for both abundance classes. We fit a model as above with abundance class as

a fixed effect to evaluate if the competition–defense correlation differed between common and rare species across all studies. We also determined if there were consistent differences within each study by fitting a regression between the correlations for common species and those for rare species.

We also investigated how the competition–defense correlation influences community structure in two ways. First, the competition–defense correlation may affect a community's response to experimental manipulations. In communities with a strong competition–defense tradeoff, the balance between resource limitation and consumer pressure maintains diversity. Removing either resource limitation or consumer pressure should therefore diminish diversity relative to control treatments. We again used log response ratios to quantify the proportional change in diversity (richness and evenness) between experimental and control treatments. We then tested for relationships between the competition–defense correlation and these diversity responses in separate linear regressions with each observation weighted by

the number of species in the community. Second, we evaluated whether those communities with a strong competition–defense tradeoff are more diverse under control conditions. To test this, we performed linear regressions (weighted as above) of studies' diversity values in control treatments against their competition–defense correlations. Diversity values were log-transformed to meet the assumption of normality. Communities artificially assembled by researchers were not included in these analyses.

1. Chesson P (2000) Mechanisms of maintenance of species diversity. *Annu Rev Ecol Syst* 31:343–366.
2. Paine RT (1966) Food web complexity and species diversity. *Am Nat* 100:65–75.
3. Lubchenco J (1978) Plant species diversity in a marine intertidal community: Importance of herbivore food preference and algal competitive abilities. *Am Nat* 112:23–39.
4. Worm B, Lotze HK, Hillebrand H, Sommer U (2002) Consumer versus resource control of species diversity and ecosystem functioning. *Nature* 417:848–851.
5. McCauley E, Briand F (1979) Zooplankton grazing and phytoplankton species richness: Field tests of the predation hypothesis. *Limnol Oceanogr* 24:243–252.
6. Morin PJ (1983) Predation, competition, and the composition of larval anuran guilds. *Ecol Monogr* 53:119–138.
7. Menge BA, Berlow EL, Blanchette CA, Navarrete SA, Yamada SB (1994) The keystone species concept: Variation in interaction strength in rocky intertidal habitat. *Ecol Monogr* 64:249–286.
8. Armstrong RA (1979) Prey species replacement along a gradient of nutrient enrichment: A graphical approach. *Ecology* 60:76–84.
9. Holt RD, Grover J, Tilman D (1994) Simple rules for interspecific dominance in systems with exploitative and apparent competition. *Am Nat* 144:741–771.
10. Leibold MA (1996) A graphical model of keystone predators in food webs: Trophic regulation of abundance, incidence, and diversity patterns in communities. *Am Nat* 147:784–812.
11. Kneitel JM, Chase JM (2004) Trade-offs in community ecology: Linking spatial scales and species coexistence. *Ecol Lett* 7:69–80.
12. Leibold MA (1989) Resource edibility and the effects of predators and productivity on the outcome of trophic interactions. *Am Nat* 134:922–949.
13. McPeek MA (1998) The consequences of changing the top predator in a food web: A comparative experimental approach. *Ecol Monogr* 68:1–23.
14. Steiner CF (2003) Keystone predator effects and grazer control of planktonic primary production. *Oikos* 101:569–577.
15. Chase J, Leibold M, Simms E (2000) Plant tolerance and resistance in food webs: Community-level predictions and evolutionary implications. *Evol Ecol* 14:289–314.
16. Tilman D (1982) *Resource Competition and Community Structure* (Princeton Univ Press, Princeton, NJ).
17. Levine JM, Brewer JS, Bertness MD (1998) Nutrients, competition and plant zonation in a New England salt marsh. *J Ecol* 86:285–292.
18. Stanley Harpole W, Tilman D (2006) Non-neutral patterns of species abundance in grassland communities. *Ecol Lett* 9:15–23.
19. Darcy-Hall TL, Hall SR (2008) Linking limitation to species composition: Importance of inter- and intra-specific variation in grazing resistance. *Oecologia* 155:797–808.
20. Hillebrand H, et al. (2007) Consumer versus resource control of producer diversity depends on ecosystem type and producer community structure. *Proc Natl Acad Sci USA* 104:10904–10909.
21. Craine JM, et al. (2002) Functional traits, productivity and effects on nitrogen cycling of 33 grassland species. *Funct Ecol* 16:563–574.
22. Chesson P, Kuang JJ (2008) The interaction between predation and competition. *Nature* 456:235–238.
23. Janzen DH (1970) Herbivores and the number of tree species in tropical forests. *Am Nat* 104:501–528.
24. Connell JH (1971) *Dynamics of Populations*, eds den Boer PJ, Gradwell GR (Pudoc, Wageningen, The Netherlands), pp 298–312.
25. Gruner DS, et al. (2008) A cross-system synthesis of consumer and nutrient resource control on producer biomass. *Ecol Lett* 11:740–755.
26. Smith B, Wilson JB (1996) A consumer's guide to evenness indices. *Oikos* 76:70–82.
27. Hedges LV, Gurevitch J, Curtis PS (1999) The meta-analysis of response ratios in experimental ecology. *Ecology* 80:1150–1156.
28. Caruso JC, Cliff N (1997) Empirical size, coverage, and power of confidence intervals for Spearman's rho. *Educ Psychol Meas* 57:637–654.
29. Viechtbauer W (2009) The metafor package: A meta-analysis package for R. Available at http://cran.r-project.org/web/packages/metafor/index.html.

Supporting Information

Viola et al. 10.1073/pnas.1007745107

SI Text

In our meta-analysis, we defined a competition–defense tradeoff as a negative correlation between resource limitation (the inverse of competitive ability) and consumer limitation (the inverse of resistance to consumers) for a group of species. We then used species-specific responses to resource addition and consumer removal as measures of limitation. This approach relies on the expectation that strong resource and consumer limitation translate into large responses following resource addition and consumer removal, respectively. The theoretical work from which the competition–defense tradeoff emerged supports these expectations. In these models, prey species compete for resources and experience predation by a shared consumer. Some species are better resource competitors (i.e., less limited by resources), whereas others are more resistant to predation (i.e., less limited by consumers). Both Holt et al. (1) and Leibold (2) have shown that densities of competing species change across a gradient of resource availability in predictable ways. When resources are scarce, only the species that is the best competitor for nutrients is present in the system. As resource supply increases, species that are inferior resource competitors (but better defended) invade and increase in density, at the expense of the superior resource competitors. These competitive but poorly defended species are favored when resources are scarce and consumer pressure is weak, whereas predation-resistant, poor resource competitors are dominant when resources are abundant and consumer pressure is high.

In addition to previous findings that lend support to our methods, we performed simulations to demonstrate explicitly that our approach is valid. Though there are countless ways to represent resource competition and predation in multispecies models, theoretical investigations of the competition–defense tradeoff have all used variations of the same model (1–4). We opted to use the formulation of Holt et al. (equation 10 in ref. 1), because their study is perhaps the most widely cited in support of the tradeoff:

$$\frac{dP}{dt} = P\left(a_1 b_1 N_1 + a_2 b_2 N_2 - c_p\right),$$

$$\frac{dN_1}{dt} = N_1\left(a_1' b_1' R - c_1' - a_1 P\right),$$

$$\frac{dN_2}{dt} = N_2\left(a_2' b_2' R - c_2' - a_2 P\right), \qquad \textbf{[S1]}$$

and

$$R = S - \frac{N_1}{b_1'} - \frac{N_2}{b_2'} - \frac{P}{b_p}.$$

A single consumer species P preys upon multiple species N_i with attack rates a_i and conversion efficiencies b_i, and experiences a density-independent mortality rate c_p. The competing prey species take up resource with affinities a_i' and conversion efficiencies b_i', and experience losses due both to predation and to density-independent mortality at rates c_i'. All prey and consumer functional responses are linear with respect to their food sources. The system is assumed to be closed, so resource dynamics are determined by a simple mass balance constraint (i.e., the amount of free resource is equal to the total quantity of resource in the system S less the quantities of resource bound in prey and consumer populations).

Holt et al. (1) show that prey coexist if and only if there is a tradeoff between competitive ability and resistance to predation. More formally, the superior resource competitor must be more vulnerable to predation and must also support a higher density of consumers than the inferior resource competitor. A species' competitive ability is given by its R^* value:

$$R_i^* = \frac{c_i'}{a_i' b_i'}. \qquad \textbf{[S2]}$$

As defined by Tilman (5), R^* is the resource concentration at equilibrium for a species grown in monoculture and in the absence of consumers. Species with low R^* values are better resource competitors (or are less limited by resource availability) than those with higher values.

Analogously, P^* is the consumer density a given species can support when grown in monoculture:

$$P_i^* = \frac{a_i' b_i' b_p}{a_i' b_i' + a_i b_p}\left(S - \frac{N_i^*}{b_i'}\right) - \frac{b_p c_i'}{a_i' b_i' + a_i b_p}, \qquad \textbf{[S3]}$$

where N^* is the prey species' own density at equilibrium. When resistance is the mechanism by which prey mitigate the impacts of predation, high values of P^* correspond to strong consumer limitation (i.e., susceptible prey support high consumer densities in monoculture and thus have high P^*, whereas resistant prey support few consumers and have low P^*). Thus, when the Holt et al. (1) tradeoff described above is operating, there is a negative correlation between prey species' R^* and P^* values.

We parameterized the system of equations (Eq. S1) with a tradeoff between competitive ability and defense for the two prey species. We incorporated resistance to predation for prey species 2 into the model by decreasing the consumer attack rate a_2. A cost to resistance was imposed by increasing this prey's density-independent death rate c_2'. Thus, species 2 had high R^* and low P^*, and vice versa for species 1 (Fig. S1). We focus on resistance because it is the sole mechanism of plant defense that has been shown to promote coexistence in combination with resource competition (4). In contrast, a tradeoff between tolerance and competitive ability causes species to promote conditions that most limit their competitor, leading to alternative stable states.

We used simulations, analogous to the two experimental manipulations used by the studies in our dataset, to show that species' responses to perturbations correctly correspond to their R^* and P^* values. To quantify consumer limitation, we reduced consumer density by increasing the consumer mortality rate c_p (Fig. S2A Lower, solid line). Likewise, to quantify resource limitation, we increased the total resource supply S (Fig. S2B Upper, solid line). Both c_p and S were increased to 10% above their basal levels beginning at $t = 250$, and held at those values for the duration of the simulations. We conducted these manipulations in separate simulations so as to measure resource and consumer limitation independently. For both manipulations, we quantified a species' response as the log ratio of its density following the perturbation to its density before the perturbation (defined at $t = 250$, when the system had equilibrated and resource supply and consumer mortality were still at their basal levels). We calculated log ratios for the entire postperturbation period of a simulation (from $t = 250$ to $t = 500$) to show how responses evolved through time.

Our expectations were confirmed by these simulations. When consumer mortality was increased, species 1 (higher P^*) benefited more than the resistant species as measured by log response

ratios (Fig. S2*A*). Though both species did increase initially, the release from consumer pressure drove a rapid and prolonged increase in the density of species 1. This release allowed species 1 to take up more of the available resource, which ultimately had a negative effect on its resource-limited competitor (Fig. 2*A* and Fig. S2*A*). In a similar manner, species 2 (higher R^*) benefited more than the better resource competitor when resource supply was increased (Fig. 2*B*). As resources became more available, species 2 was released from resource limitation and increased sharply. This caused a subsequent increase in consumer density, which drove down the density of species 1, the less-resistant prey (Fig. 2*B* and Fig. S2*B*).

To confirm that our finding did not rest solely on parameter selection, we conducted 1,000 simulations in which all parameters were drawn from uniform distributions ranging $\pm 20\%$ around their values in Fig. S2. We discarded simulations in which species did not coexist because they are not relevant to exploring species' relative limitation when a tradeoff maintains diversity. The species more limited by a given factor should always have a more positive response when the degree of limitation is reduced. Therefore, when consumer mortality was increased, we calculated the log response of species 1 (susceptible to consumers) minus the log response of species 2 (resistant to consumers). Likewise, when resource supply was increased, we calculated the log response of species 2 (weak resource competitor) minus the log response of species 1 (strong resource competitor). All differences were calculated at the end of the simulation ($t = 500$). These differences should always be positive if the metrics used in our paper are supported by the model, and indeed that is what we found (Fig. S3).

From such simulations, we conclude that log response ratios to resource addition and consumer removal are valid metrics of resource and consumer limitation, respectively. Though the sign of a species' log response ratio did sometimes change over time, relative to one another, species' responses were always what we would expect. That is, the species more limited by a given factor always benefits more when that limitation is removed. For example, species 2 was resistant to predation, yet did have a brief positive response to consumer removal. Crucially, although, the response of species 1, the consumer-limited species, was always greater than that of species 2 throughout the postperturbation period (i.e., the blue curve in Fig. 2*A* is always above the green curve).

1. Holt RD, Grover J, Tilman D (1994) Simple rules for interspecific dominance in systems with exploitative and apparent competition. *Am Nat* 144:741–771.
2. Leibold MA (1996) A graphical model of keystone predators in food webs: Trophic regulation of abundance, incidence, and diversity patterns in communities. *Am Nat* 147:784–812.
3. Grover JP, Holt RD (1998) Disentangling resource and apparent competition: Realistic models for plant-herbivore communities. *J Theor Biol* 191:353–376.

4. Chase J, Leibold M, Simms E (2000) Plant tolerance and resistance in food webs: Community-level predictions and evolutionary implications. *Evol Ecol* 14:289–314.
5. Tilman D (1982) *Resource Competition and Community Structure* (Princeton Univ Press, Princeton, NJ).

Studies Used in the Meta-Analysis

1. Buckland SM, Grime JP (2000) The effects of trophic structure and soil fertility on the assembly of plant communities: A microcosm experiment. *Oikos* 91:336–352.
2. Carreiro-Silva M, McClanahan TR, Kiene WE (2005) The role of inorganic nutrients and herbivory in controlling microbioerosion of carbonate substratum. *Coral Reefs* 24:214–221.
3. Davis BNK, Lakhani KH, Brown MC (1993) Experiments of the effects of fertilizer and rabbit grazing treatments upon the vegetation of a limestone quarry floor. *J Appl Ecol* 30:615–628.
4. Díaz S, Fraser LH, Grime JP, Falczuk V (1998) The impact of elevated CO_2 on plant-herbivore interactions: Experimental evidence of moderating effects at the community level. *Oecologia* 117:177–186.
5. Fraser LH, Grime JP (1998) Top-down control and its effect on the biomass and composition of three grasses at high and low soil fertility in outdoor microcosms. *Oecologia* 113:239–246.
6. Fraser LH, Grime JP (1999) Interacting effects of herbivory and fertility on a synthesized plant community. *J Ecol* 87:514–525.
7. Gough L, Grace JB (1998) Herbivore effects on plant species density at varying productivity levels. *Ecology* 79:1586–1594.
8. Grellmann D (2002) Plant responses to fertilization and exclusion of grazers on an arctic tundra heath. *Oikos* 98:190–204.
9. Hagerthey SE, Defew EC, Paterson DM (2002) Influence of *Corophium volutator* and *Hydrobia ulvae* on intertidal benthic diatom assemblages under different nutrient and temperature regimes. *Mar Ecol Prog Ser* 245:47–59.
10. Hill WR, Boston HL, Steinman AD (1992) Grazers and nutrients simultaneously limit lotic primary productivity. *Can J Fish Aquat Sci* 49:504–512.
11. Hillebrand H, Worm B, Lotze HK (2000) Marine microbenthic community structure regulated by nitrogen loading and grazing pressure. *Mar Ecol Prog Ser* 204:27–38.
12. John E, Turkington R (1995) Herbaceous vegetation in the understorey of the boreal forest: Does nutrient supply or snowshoe hare herbivory regulate species composition and abundance. *J Ecol* 83:581–590.
13. Liess A, Kahlert M (2007) Gastropod grazers and nutrients, but not light, interact in determining periphytic algal diversity. *Oecologia* 152:101–111.

14. McCormick PV, Stevenson RJ (1989) Effects of snail grazing on benthic algal community structure in different nutrient environments. *J N Am Benthol Soc* 8:162–172.
15. McCormick PV, Stevenson RJ (1991) Grazer control of nutrient availability in the periphyton. *Oecologia* 86:287–291.
16. Perez-Martinez C, Cruz-Pizarro L (1995) Species-specific phytoplankton responses to nutrients and zooplankton manipulations in enclosure experiments. *Freshwater Biol* 33:193–203.
17. Rosemond AD, Mulholland PJ, Brawley SH (2000) Seasonally shifting limitation of stream periphyton: response of algal populations and assemblage biomass and productivity to variation in light, nutrients, and herbivores. *Can J Fish Aquat Sci* 57:66–75.
18. Steinman AD (1992) Does an increase in irradiance influence periphyton in a heavily-grazed woodland stream? *Oecologia* 91:163–170.
19. Steinman AD, McIntire CD, Gregory SV, Lamberti GA (1989) Effects of irradiance and grazing on lotic algal assemblages. *J Phycol* 25:478–485.
20. Steinman AD, Mulholland PJ, Kirschtel DB (1991) Interactive effects of nutrient reduction and herbivory on biomass, taxonomic structure, and P-uptake in lotic periphyton communities. *Can J Fish Aquat Sci* 48:1951–1959.
21. Sumner WT, McIntire CD (1982) Grazer-periphyton interactions in laboratory streams. *Arch Hydrobiol* 93:135–157.
22. Thacker R, Ginsburg D, Paul V (2001) Effects of herbivore exclusion and nutrient enrichment on coral reef macroalgae and cyanobacteria. *Coral Reefs* 19:318–329.
23. Turkington R, John E, Watson S, Seccombe-Hett P (2002) The effects of fertilization and herbivory on the herbaceous vegetation of the boreal forest in north-western Canada: A 10-year study. *J Ecol* 90:325–337.
24. Walton SP, Welch EB, Horner RR (1995) Stream periphyton response to grazing and changes in phosphorus concentration. *Hydrobiologia* 302:31–46.
25. Wellnitz TA, Rader RB, Ward JV (1996) Light and a grazing mayfly shape periphyton in a Rocky Mountain stream. *J N Am Benthol Soc* 15:496–507.
26. Worm B, et al. (1999) Marine diversity shift linked to interactions among grazers, nutrients and propagule banks. *Mar Ecol Prog Ser* 185:309–314.
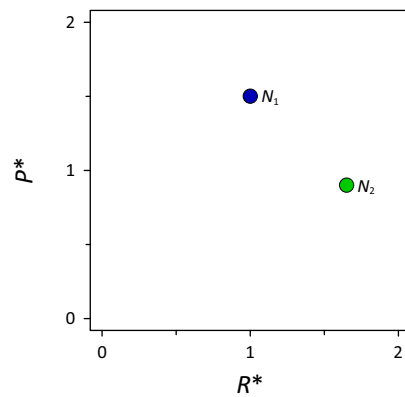
Fig. S1. R^* and P^* values of two species with a competition–defense tradeoff. Species 1 is the better competitor but is more susceptible to predation. Species 2 has greater resistance to consumers but is poorer at resource exploitation.
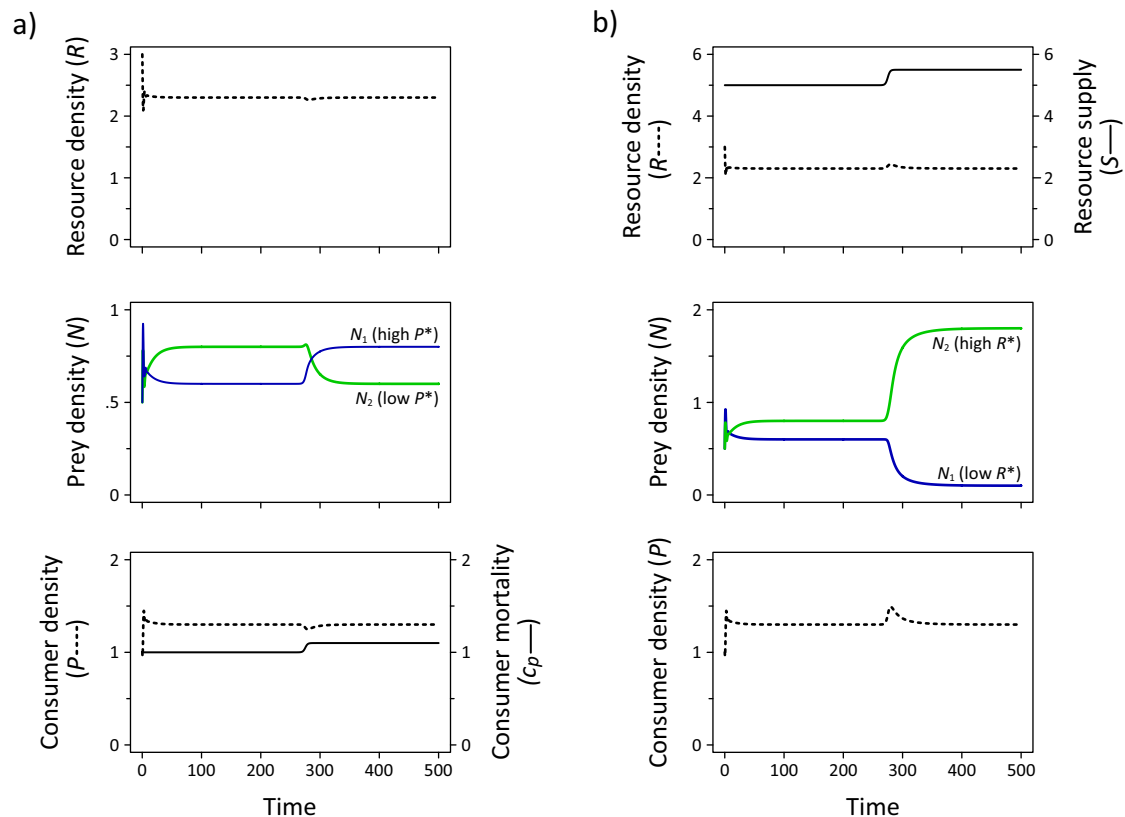
Fig. S2. Representative simulations of the Holt et al. model (Eq. S1) with perturbations in (*A*) consumer mortality and (*B*) resource supply. For both cases, we first allowed the system to equilibrate. To evaluate how limited species were by predation, we imposed an increase in consumer mortality c_p to 10% above its basal level (*A, Lower*). To evaluate resource limitation, we increased the resource supply S to 10% above its basal level (*B, Upper*). All other parameters in Eq. S1 were set to 1 except $a_2 = 0.5$, $c_2' = 1.625$, and $S = 5$.
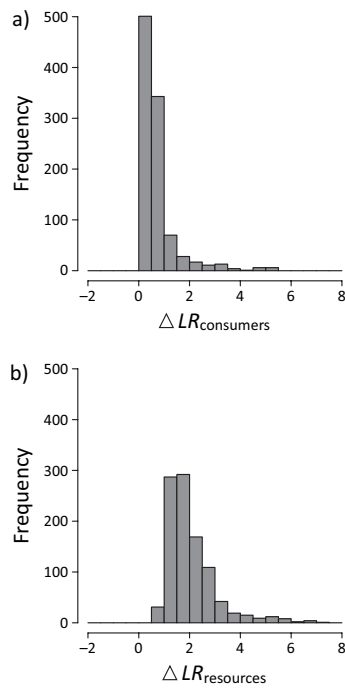
Fig. S3. Differences between species' log response ratio to (*A*) an increase in consumer mortality and to (*B*) an increase in resource supply when model parameters varied randomly. In *A*, the *x* axis is the response of species 1 (susceptible to consumers) minus the response of species 2 (resistant to consumers). In *B*, the *x* axis is the response of species 2 (weak resource competitor) minus the response of species 1 (strong resource competitor). Positive values indicate model support for our metrics of competitive ability and consumer resistance.
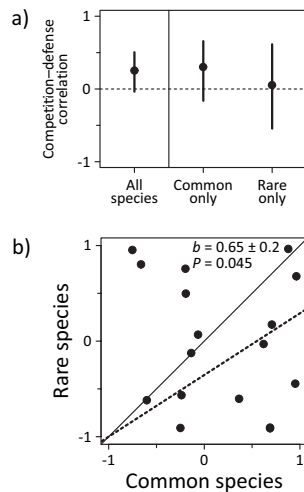
Fig. S4. Tradeoffs tend to be stronger among the rarest species in a community. (*A*) Mean competition–defense correlations did not differ significantly regardless of whether all species were included in the correlation, or whether only common or rare species were included. However, (*B*) competition–defense correlations within each study were consistently lower for rare species than for common species. The fitted line (dashed) falls below the 1:1 line (solid; the expected relationship if correlations for common and rare species within a study were equal on average). The *P* value is for the test that the estimated slope equals 1.

Fig. S5. Competition–defense correlations (±SE) over time for studies with time-series data. SEs are symmetrical, but are truncated for presentation in the cases for which bars fall outside the range of the correlation coefficient. Data are from (*A*) Thacker et al. (1); (*B*) Perez-Martinez and Cruz-Pizarro (2); (*C*) Steinman et al. (3); (*D*) Sumner and McIntire (4); (*E*) Walton et al. (5); (*F*) Steinman (6); and (*G*) Steinman et al. (7). See Studies Used in the Meta-Analysis for full citations.

Table S1. Definitions of variables

Variable	Definition
Ecological characteristics	
System type	The habitat of the study (freshwater, marine, or terrestrial)
Organismal complexity	A broad classification of study organism (single cellular or multicellular)
Resource	The resource that was manipulated (light, nitrogen, or phosphorous, and in combinations)
Consumer	A broad classification of the type of consumer that was manipulated (invertebrate or vertebrate)
Experimental characteristics	
Study venue	The experimental location of the study (laboratory, field, or mesocosm)
Community assembly	The way in which the community was formed (artificial or natural)
Response variable	The way in which species' responses were measured (e.g., percent cover or biomass)
Duration	The number of days after treatments were imposed when response variable measured
Treatment definitions	
Control	Unfertilized and with consumers present
Resource addition	Fertilized and with consumers present
Consumer removal	Unfertilized and with consumers reduced or removed
Species-level variables	
Resource response	Log ratio of abundance in resource addition treatment to abundance in control treatment
Consumer response	Log ratio of abundance in consumer removal treatment to abundance in control treatment
Community-level variables	
Community size	No. of species in a study
Evenness	Species evenness for a given treatment
Richness	Species richness for a given treatment
Competition–defense correlation	Correlation between resource response and consumer response

Table S2. Test statistics for fixed categorical effects

Factor	Q	df	P
System type	3.87	2	0.144
Organismal complexity	0.88	1	0.347
Resource	3.48	4	0.481
Consumer	1.28	1	0.257
Study venue	0.31	2	0.854
Community assembly	0.29	1	0.588
Response variable	0.25	3	0.970

Q statistics are approximately χ^2 distributed with degrees of freedom (df).

Table S3. Test statistics for overall residual heterogeneity within levels of categorical effects

Factor	Q	df	P
Overall	95.35	35	
System type			
Terrestrial	49.05	9	<0.001
Freshwater	26.21	17	0.071
Marine	23.12	7	0.002
Organismal complexity			
Multicellular	43.19	10	<0.001
Single cellular	50.41	24	0.001
Resource			
Light (L)	1.70	3	0.637
Nitrogen (N)	19.33	2	<0.001
Phosphorous (P)	1.98	2	0.372
N + P	65.17	23	<0.001
L + N + P	2.96	1	0.085
Consumer			
Vertebrate	19.73	6	0.003
Invertebrate	74.08	28	<0.001
Study venue			
Laboratory	15.50	8	0.050
Field	51.38	22	<0.001
Mesocosm	30.57	3	<0.001
Community assembly			
Natural	56.02	22	<0.001
Artificial	41.78	12	<0.001
Response variable			
Biomass	34.88	5	<0.001
Percent cover	32.08	13	<0.001
Abundance	7.38	9	0.597
Biovolume	23.33	5	<0.001

Q statistics are approximately χ^2 distributed with degrees of freedom (df).